ISOLATED GRAPTOLITES FROM THE LLANDOVERY OF KALLHOLEN, SWEDEN

by D. K. LOYDELL

ABSTRACT. A graptolite fauna of *Monograptus argenteus* Biozone age (Aeronian = Middle Llandovery), chemically isolated from limestone nodules formerly thought to be of *M. turriculatus* Biozone age (Telychian = Upper Llandovery), is described. The total fauna comprises *Metaclimacograptus hughesi* (Nicholson), *Glyptograptus* aff. *incertus* Rickards, *G. sinuatus sinuatus* (Nicholson), *Clinoclimacograptus retroversus* Bulman and Rickards, *Agetograptus primus* Obut and Sobolevskaya, *Agetograptus* sp., '*Orthograptus*' *cyperoides* (Törnquist), '*O.*' *insectiformis* (Nicholson), *Monoclimacis* sp., *Pristiograptus concinnus* (Lapworth), *Pribylograptus leptotheca* (Lapworth), *Monograptus communis communis* Lapworth, *M. denticulatus sensu* Sudbury, *M. millepeda* M'Coy and *Rastrites peregrinus* Barrande. Spines are recognized for the first time on the thecae of *M. c. communis* and *M. millepeda*. It is suggested that *M. lobiferus* evolved from *M. millepeda* which had itself evolved from *M. c. communis*. The generic diagnosis for *Pribylograptus* Obut and Sobolevskaya is emended, as the existing diagnosis for the genus is based upon a misinterpretation of the thecal structure derived from examination of pyrite internal moulds.

IN 1970, Hutt, Rickards and Skevington described a number of graptolites (eleven species in total) chemically isolated from limestone nodules from the *turriculatus* Biozone of Osmundsberget, Dalarna, Sweden. When similar material, collected by Drs M. G. Bassett, R. B. Rickards and J. Gluyas became available, it seemed an ideal opportunity to compare uncrushed, isolated material with the common low-relief internal moulds and rare flattened rhabdosomes found in Wales. Such study would aid interpretation of, in particular, the thecal structures of such imperfect material.

Dr Bassett also provided limestone nodules from Kallholen (also in Dalarna), which were considered (pers. comm.) to come from a similar horizon to the Osmundsberget nodules. However, the recognition of species such as *Monograptus millepeda* (M'Coy, 1850) and *Pribylograptus leptotheca* (Lapworth, 1876) in the residues of some of the first samples processed indicated that this was not the case, and that the Kallholen nodules contained a fauna from rather earlier in the Llandovery, from the Aeronian *M. argenteus* Biozone.

The vast majority of the species extracted from these nodules have never before been described in isolated condition and thus a large amount of new (and often surprising) morphological information, in some cases of considerable taxonomic importance, has been derived.

TECHNIQUES

The isolation techniques used are fully described in Dumican and Rickards (1985) and in Bates *et al.* (1988). The nodules were dissolved in acetic acid as this has a less effervescent reaction with carbonate than hydrochloric acid, and thus causes less damage to emerging specimens. Some specimens were cleared (i.e. rendered transparent) using the technique described by Berry (pp. 106–107, in Kummel and Raup 1965). Initial examination under a light microscope was followed by more detailed study with a scanning electron microscope (SEM) again using the techniques described in Dumican and Rickards (1985).

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PREVIOUS WORK ON ISOLATED NON-RETIOLITE LLANDOVERY GRAPTOLITES

Any retiolite graptolites isolated from the nodules were passed to Drs Bates and Kirk. The following account of previous research therefore considers only monograptids and 'normal' diplograptids.

Other than Hutt, Rickards and Skevington's (1970) work, which also included descriptions of seven species from the *Coronograptus gregarius* Biozone (Aeronian) of Silvberg, also in Dalarna, Sweden, little work has been published on isolated non-retiolite Llandovery graptolites, although undoubtedly a wealth of material exists, particularly from the Canadian Arctic. This dearth of studies is surprising, for as Fortey (1989) states: 'One good isolated fossil fauna is worth any amount of speculation on structure and phylogenetics based on flattened specimens.'

Bulman (1932) described three monograptid species from the *Retiolites*-Shales of Stygforsen, Dalarna, Sweden, which had been prepared by Holm in the latter part of the nineteenth century. Two of these he assigned to *Monograptus priodon* (Bronn, 1835) and *M. spiralis* (Geinitz, 1842). The third he was unable to identify. It is herein recognized as *Streptograptus grayae* (Lapworth, 1876).

Lenz (1974) analysed evolutionary trends within *M. priodon* from the uppermost Llandovery to lower Wenlock, using isolated material from Cornwallis Island, Arctic Canada.

Paškevičius (1976) erected the genus *Litluanograptus* on the basis of examination of isolated Rhuddanian and Aeronian diplograptaceans from Lithuania, USSR. It is probable that many of his specimens are simply flattened metaclimacograptids.

In 1977, Rickards, Hutt and Berry illustrated thecae considered by them to be from *M. delicatulus* Elles and Wood, 1913. Crowther (1981) described *Paraclimacograptus innotatus innotatus* (Nicholson, 1869) from the Dergaish River, south Ural Mountains, USSR, and *Dimorphograptus*? sp. from Cornwallis Island, Canada.

Obut and Sennikov (1980) described a number of *Monograptus triangulatus* Biozone (Aeronian) monograptid and diplograptid taxa from the Siberian Platform, USSR. Their fine material would certainly benefit from further examination with an SEM.

Bates and Kirk (1984) gave a description and discussed the probable function of ancoras from three different diplograptid species. Their suggestion of horizon as ? *M. turriculatus* Zone for this Kallholen material is, as mentioned above, now known to be incorrect.

Melchin and Lenz (1986) described *M. turriculatus* (Barrande, 1850) from Cornwallis Island, and discussed its possible derivation from *M. sedgwickii* (Portlock, 1843). Chen (1986*a*) described seven generally poorly preserved species from the Aeronian of Yichang, W Hubei, China. This material was extracted from siliceous marl concretions by dissolution first in hydrochloric and then hydrofluoric acid. Chen (1986*b*) has also described isolated material of *Streptograptus plumosus* (Baily, 1871) (misidentified by him as *S. nodifer* (Törnquist, 1881)) from north-east Guizhou, and further work on isolated faunas is in progress.

Most recently, Lenz and Melchin (1989) have described uncompressed specimens of *M. spiralis* again from Cornwallis Island, and suggest that this species is unlikely to be ancestral to the genus *Cyrtograptus* Carruthers, 1867, three isolated species of which they also describe – *C. sakmaricus* Koren', 1968, *C.* sp. and *C.* cf. *C. laqueus* Jackson and Etherington, 1969.

LOCALITY INFORMATION

As Kallholen has not been visited by the author, the information below is derived entirely from Bassett (pers. comm. to D. Bates).

The graptolites were isolated from nodules from the lowest band exposed (within basal 2 m) in the Llandovery sequence unconformably overlying the Upper Ordovician Boda Limestone. The nodules were collected from sections on both sides of the western entrance to the quarry on the east side of road 296, directly opposite Kallholen limestone works, 7·5 km NE of Orsa Church, Siljan district, Dalarna (UTM Grid reference VH 8440 8153).

SYSTEMATIC PALAEONTOLOGY

The terminology used is mainly that of Bulman (1970). Thecal spacing is expressed in terms of a two theca repeat distance (2TRD), as defined by Howe (1983).

Synonymies are brief for the well-known taxa, as more complete synonymies may be found in, for example, Rickards (1970) and Hutt (1974, 1975). They are annotated with the symbols proposed by Richter (1948) and Rabien (1954), summarized in Matthews (1973).

Suprageneric classification is based on Mitchell (1987), with reservation, particularly with regard to the lowly status conferred by Mitchell (*op. cit.*) upon the 'monograptids'.

All material figured in the plates is housed in the Institute of Earth Studies, University College of Wales, Aberystwyth.

Repositories of type material are abbreviated as follows: BM (NH) – Natural History Museum; BU – Birmingham University; SM – Sedgwick Museum, Cambridge.

Order GRAPTOLOIDEA Lapworth, 1873
Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTACEA Lapworth, 1873 (emend. Mitchell, 1987)
Family GLYPTOGRAPTIDAE Fortey and Cooper, 1986
Subfamily GLYPTOGRAPTINAE Fortey and Cooper, 1986
Genus GLYPTOGRAPTUS Lapworth, 1873 (emend. Mitchell, 1987)

Type species. Original designation; *Diplograpsus tamariscus* Nicholson, 1868, p. 526, pl. 19, figs 10–13.

Glyptograptus aff. *incertus* Rickards, 1970

Plate 1, fig. 1

1970 *Glyptograptus* aff. *incertus* (Elles and Wood, 1907); Rickards pp. 40–41, text-fig. 14, fig. 11.
p1974 *Glyptograptus* (*G.*) *incertus* (Elles and Wood, 1907); Hutt, p. 25, pl. 3, fig. 3; pl. 4, fig. 13 (*non* 12); text-fig. 8, fig. 11.

Material. One specimen.

Description. The 4·5 mm long specimen has been laterally compressed producing a corrugated appearance along its midline. The thecae have sharp genicula on th1[1]–3[2]. There is then an abrupt change to sigmoidally curved thecae and flowing, rounded genicula. Thecal apertures are horizontal. Dorso-ventral width increases from 0·5 mm at th1[1] to 1 mm at th5[1]. 2TRD ranges from 1·3 to 1·5 mm.

Remarks. The specimen agrees very well with the material illustrated by Rickards (1970) and Hutt (1974). *G. incertus* Elles and Wood, 1907 differs in having a broader, more rounded proximal end and also in that the geniculum becomes less angular more gradually along the length of the rhabdosome. The latter species is fully described by Packham (1962).

Glyptograptus sinuatus sinuatus (Nicholson, 1869)

Plate 1, fig. 2

*.1869 *Diplograpsus sinuatus* Nicholson, p. 235, pl. 11, fig 11.
1907 *Diplograptus* (*Glyptograptus*) *sinuatus* Nicholson; Elles and Wood, pp. 255–257, pl. 31, fig. 6; text-fig. 175.
.1970 *Glyptograptus sinuatus sinuatus* (Nicholson); Rickards, pp. 41–42, pl. 4, fig. 1.
.1974 *Glyptograptus* (*G.*) *sinuatus sinuatus* (Nicholson); Hutt, p. 28, pl. 4, figs 1–4, 10.
.1975 *Glyptograptus sinuatus sinuatus* (Nicholson); Bjerreskov, p. 31, pl. 4, fig. D.

Holotype. By monotypy; specimen figured Nicholson 1869, pl. 11, fig. 11; from the Llandovery of Skelgill, the English Lake District.

Material. Several proximal ends, and a few more fully developed rhabdosomes.

Description. The rhabdosome increases in width fairly rapidly from 0·5–0·6 mm at th1[1] to 1·3 mm at th5[1]. 2TRD is 1·35–1·5 mm at th2[1], and 1·5–1·55 mm at th5[1]. The first three thecal pairs have sharp genicula and straight supragenicular walls inclined at a very low angle to the rhabdosome axis. An abrupt change in thecal morphology then occurs, all further thecae being sigmoidally curved with flowing genicula.

Remarks. The abrupt change in the thecal morphology has been widely illustrated. This species, perhaps more than any other, illustrates the futility of the traditional diplograptacean generic classification (see Bulman 1970) which was based largely on thecal morphology. The character of the proximal thecae of this species would place it in *Climacograptus* Hall, 1865, whilst that of the distal thecae would place it in *Glyptograptus* Lapworth, 1873. As a result of the work of Fortey and Cooper (1986) and Mitchell (1987) this traditional classification has now been abandoned in favour of one which is phylogenetically based, concentrating on early astogenetic development.

Genus CLINOCLIMACOGRAPTUS Bulman and Rickards, 1968.

Type species. Original designation; *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* Bulman and Rickards, 1968, p. 8; from the Llandovery of Sweden and Britain.

Clinoclimacograptus retroversus Bulman and Rickards, 1968

Plate 1, figs 5 and 14

1893 *Climacograptus scalaris* Lin.; Törnquist, pp. 2–6, figs 1–3, 5–8, 11–15, ? 4, 9, 10, 16–22.
*.1968 *P.* (*Clinoclimacograptus*) *retroversus* Bulman and Rickards, pp. 8–12, text-figs 3–5.
.1970 *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* Bulman and Rickards; Rickards, pp. 34–35, text-fig. 14, figs 1–4.
.1974 *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* Bulman and Rickards; Hutt, p. 23, pl. 2, figs 10–12.
.1975 *Pseudoclimacograptus retroversus* (Bulman and Rickards); Bjerreskov, pp. 25–26, text-fig. 9D, E.

Holotype. Original designation; figured Bulman and Rickards 1968, fig. 4*b*; SM A52951; from Tomarp Sweden, probably *M. sedgwickii* Biozone.

Material. Approximately 200 specimens.

Description. The rhabdosome is essentially parallel-sided, increasing in dorso-ventral width only very gradually from 0·6–0·8 mm at th1[1] to a distal maximum of 1·1–1·35 mm, although some specimens exhibit a slight subsequent reduction in width (as shown by specimen UCWG961B, figured Pl. 1, fig. 14). 2TRD increases from 1·2–1·4 mm at th2[1] to 1·45–1·6 mm distally. The thecae have sharp genicula and characteristic slightly concave supragenicular walls. The apertures alternate and are horizontal or very slightly introverted. Their excavations each comprise *c.* one-tenth of the dorso-ventral width for the first thecal pair, increasing to *c.* one-fifth distally. The median septum (seen on cleared specimens) is gently undulating proximally, becoming almost straight distally.

Remarks. The material agrees well with Bulman and Rickards's (1968) description other than in its attainment of a greater distal width. In this respect it resembles *Pseudoclimacograptus* (*Clinoclimacograptus*)? *washingtoni* Bjerreskov, 1981, but this latter species has a narrower proximal end and more widely spaced thecae. Bulman and Rickards (1968) noted the long range of *Cl. retroversus* (*M. triangulatus* to *M. sedgwickii* Biozones) and suggested that it might be possible to subdivide it into a number of stratigraphically useful forms.

Genus METACLIMACOGRAPTUS Bulman and Rickards, 1968

Type species. Original designation; *Diplograpsus Hughesi* Nicholson, 1869, p. 235, pl. 11, figs 9 and 10; from the Llandovery of the Lake District, England.

Metaclimacograptus hughesi (Nicholson, 1869)

Plate 1, figs 3, 4, 6, 9, 12

*.1869 *Diplograpsus Hughesi* Nicholson, p. 235, pl. 11, figs 9 and 10.
1906 *Climacograptus Hughesi* Nicholson; Elles and Wood, pp. 208–210, pl. 27, fig. 11; text-fig. 140.
.1968 *P. (Metaclimacograptus) hughesi* (Nicholson); Bulman and Rickards, pp. 3–6, fig. 1.
.1970 *Pseudoclimacograptus (Metaclimacograptus) hughesi* (Nicholson); Rickards, p. 33, text-fig. 14, fig. 6.
.1970 *P. (Metaclimacograptus) hughesi* (Nicholson); Hutt, Rickards and Skevington, p. 4, pl. 1, figs 1–4.
1974 *Pseudoclimacograptus (Metaclimacograptus) hughesi* (Nicholson); Hutt, p. 22, pl. 2, figs 6, 7, 13, 14.
1975 *Pseudoclimacograptus undulatus* (Kurck, 1882); Bjerreskov, p. 26, pl. 4, fig E.

Neotype. Designated Přibyl 1948, p. 18, as the specimen figured by Elles and Wood 1906, pl. 27, fig. 11*a*; BM (NH) P1890.

Material. Several hundred specimens.

Description. The rhabdosome appears essentially parallel-sided, its width increasing very gradually from 0·5–0·6 mm at th1[1] to a distal maximum of 0·75 mm. 2TRD is 1·0–1·25 mm at th2[1]. Distally it lies between 1·2 and 1·5 mm. The thecae have sharp, slightly overhanging and thickened genicula. Their apertures alternate. They are introverted, with excavations comprising *c*. one-third of the rhabdosome's dorso-ventral width. The medium septum (seen on cleared specimens) undulates.

One specimen has a circular cyst-like growth on the obverse side of the rhabdosome close to the aperture of th2[1] (Pl. 1, figs 3 and 6).

Remarks. Bulman and Rickards (1968) describe this species in great detail. The thickening of the geniculum is presumably the same structure as the genicular hood described in this species by Bulman and Rickards (*op. cit.*). Hutt, Rickards and Skevington (1970) noted faint traces of genicular hoods on some of their isolated, but flattened, material.

The cyst-like growth may be the result of parasitism. Similar growths have been recognised before, for example by Jackson (1971). Conway Morris (1981) gives a useful review of parasitism in the fossil record, which includes examples on graptolites.

Subfamily RETIOLITINAE Lapworth, 1973 (emend. Mitchell, 1987)
Genus AGETOGRAPTUS Obut and Sobolevskaya, 1968

Type species. Original designation; *Agetograptus secundus* Obut and Sobolevskaya (in Obut, Sobolevskaya and Merkureva 1968), pp. 79–80, pl. 8, figs 9–12; pl. 9, figs 1–13; pl. 10, figs 1–5; from the Llandovery of a borehole in the Norilsk region, USSR.

Diagnosis. Species with th1[2] longer than th1[1] and 2[1] so that its aperture is higher than that of th2[1]. Throughout the rhabdosome the aperture of the thecae of the second series open above the succeeding thecae of the first series.

Remarks. Bulman (1970) placed this genus into synonymy with *Dimorphograptus* Lapworth, 1876. However, it differs from this genus in that in *Agetograptus* th1[2] is elongated rather than being suppressed. The superficial appearance of the proximal end is similar in both genera.

Rickards, Hutt and Berry (1977, p. 25) note that some specimens of *Ag. secundus* have a normal proximal end (i.e. thecal apertures alternating). Neither of the species described herein exhibits this feature, however, which Rickards, Hutt and Berry (*op. cit.*) consider as being indicative of a dithyrial population (Jaanusson 1973).

Agetograptus primus Obut and Sobolevskaya, 1968

Plate 1, figs 11, 16, 18, 19; Plate 2, fig. 2

*.1968	*Agetograptus primus* Obut et Sobolevskaya; Obut, Sobolevskaya and Merkureva, pp. 80–1, pl. 10, figs 6–12.
1970	*Orthograptus bellulus* Törnquist; Churkin and Carter, p. 28, pl. 3, fig. 1; text-fig. 12G.
?1970	*Orthograptus* cf. *insectiformis* (Nicholson, 1869); Rickards, pp. 46–47, text-fig. 14, fig. 18.
p1978	*Orthograptus insectiformis* (Nicholson); Chen and Lin, p. 39, pl. 7, fig. 3 (*non* 1 and 2).

Holotype. By original designation, the specimen illustrated by Obut, Sobolevskaya and Merkureva 1968, pl. 10, fig. 6, from the Middle Llandovery of borehole N-1, Norilsk district, USSR.

Material. Approximately 100 specimens.

Description. The rhabdosome increases moderately rapidly in dorso-ventral width from 0·4–0·65 mm at th1[1] to 0·9–1·2 mm at th5[1], the maximum distal value recorded being 1·9 mm. 2TRDs are characteristically low, 0·65–0·9 mm at th2[1], increasing to 1·15–1·4 mm distally. The thecae are straight tubes inclined at *c.* 30° to the rhabdosome axis. Each aperture bears a pair of short, gently curving spines directed antero- and posterio-laterally. These are situated on the dorsal margin of the aperture. The virgella is long and robust.

Remarks. The position of the spines results in them being visible only when an oblique or lateral view is presented. They were not observed by Obut and Sobolevskaya (1968) in their material.

Poorly preserved specimens of *Ag. primus* might easily be mistaken for '*Orthograptus*' *bellulus* (Törnquist, 1890).

EXPLANATION OF PLATE 1

Fig. 1. *Glyptograptus* aff. *incertus* Rickards, 1970, UCWG961C, obverse view; note lateral compression, ×10.

Fig. 2. *Glyptograptus sinuatus* (Nicholson, 1869), UCWG943B, obverse view, ×10.

Figs 3, 4, 6, 9, 12. *Metaclimacograptus hughesi* (Nicholson, 1869), 3, UCWG956B, obverse view; note cyst-like structure adjacent to aperture of th2[1], ×10. 4, UCWG919A, obverse view; ×20. 6, UCWG956B, cyst-like structure, ×100. 9, UCWG930D, early growth stage, ×50. 12, UCWG930C, thecal aperture, ×75.

Figs 5 and 14. *Clinoclimacograptus retroversus* Bulman and Rickards, 1968. 5, UCWG943A, obverse view; ×10. 14, UCWG961B, distal fragment showing slight narrowing of rhabdosome and decrease in angularity of geniculum, ×10.

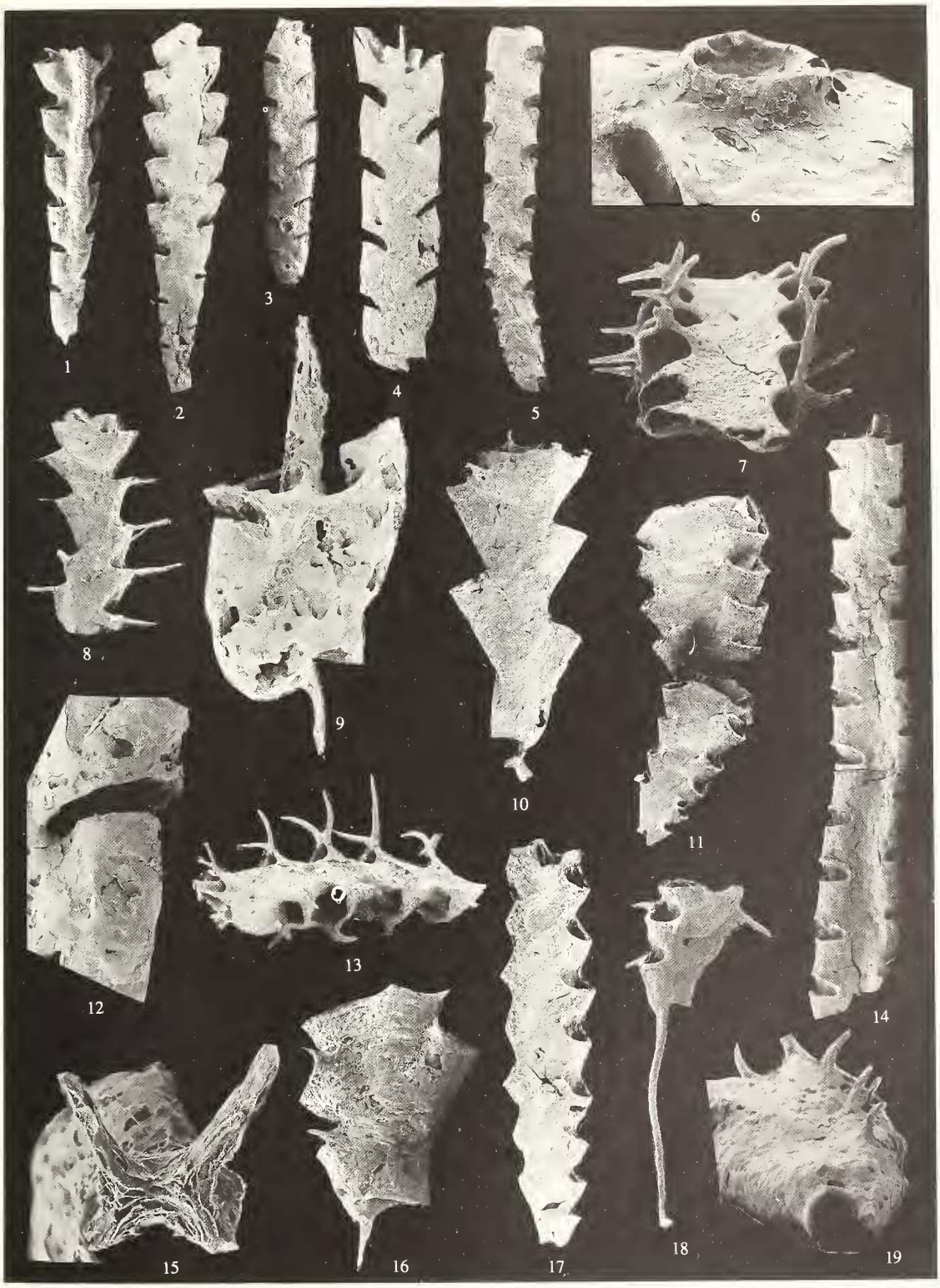
Figs 7, 8, 13. '*Orthograptus*' *insectiformis* (Nicholson, 1869). 7, UCWG956D, viewed from distal end of rhabdosome, ×20. 8, UCWG956A, mesial fragment, ×10. 13, UCWG956A, showing form of thecal apertures and spines, ×15.

Figs 10 and 15. '*Orthograptus*' *cyperoides* (Törnquist, 1897). 10, UCWG1027, reverse view, ×20. 15, UCWG1027, ancora, ×150.

Figs 11, 16, 18, 19. *Agetograptus primus* Obut and Sobolevskaya, 1968. 11, UCWG911B, reverse view, ×10. 16, UCWG960D, early growth stage, ×40. 18, UCWG958C, early growth stage; note long, robust virgella, ×40. 19, UCWG911B, view from proximal end; note thecal spines, ×20.

Fig. 17. *Agetograptus* sp., UCWG919D, reverse view, ×15.

All scanning electron micrographs.



LOYDELL, Swedish Llandovery graptolites

Agetograptus sp.

Plate 1, fig. 17; Plate 2, figs 1 and 3

Material. Two specimens.

Description. The rhabdosome is gently tapering. Its dorso-ventral width increases from 0·5–0·55 mm at th1[1] to 0·9–1·0 mm at th5[1]. 2TRD at th2[1] is 0·75 mm. At th5[1] it is 1·1 mm. The thecae are simple tubes, inclined at *c.* 25° to the rhabdosome axis, with slightly everted thecal apertures. The nema is partially enclosed in a sheath-like structure (Pl. 2, fig. 1).

Remarks. This species is similar to *Ag. tenuilongissimus* Obut and Sobolevskaya, 1968 but has more closely spaced thecae.

Genus 'ORTHOGRAPTUS' Lapworth, 1873

'*Orthograptus*' *cyperoides* (Törnquist, 1897)

Plate 1, figs 10 and 15

*.1897	*Diplograptus cyperoides* Törnquist, p. 16, pl. 2, figs 30–32.
1907	*Diplograptus* (*Orthograptus*) *cyperoides* Törnquist; Elles and Wood, pp. 238–239, pl. 29, fig. 8; text-fig. 158.
1970	*Orthograptus cyperoides* (Törnquist); Rickards, pp. 45–46, text-fig. 14, figs 12 and 17.
?1974	*Orthograptus cyperoides* (Törnquist); Hutt, p. 35, pl. 6, figs 2–5; text-fig. 9, figs 6 and 7.
?1975	*Orthograptus cyperoides* (Törnquist); Bjerreskov, pp. 28–29, text-fig. 10D.
.1985	*Orthograptus cyperoides* (Törnquist); Storch, p. 90, pl. 1, figs 1–4, (? 5); text-fig. 2F, G.

Type specimen. Not yet designated. Törnquist's material was from the *cometa* Biozone of Tomarp, Sweden.

Material. One specimen, a proximal end, bearing thecae up to th3[1].

Description. The specimen has a width of 0·8 mm at th1[1] and 0·9 mm at th2[1]. The simple thecae are inclined at 30° to the rhabdosome axis and have apertures almost perpendicular to the thecal axis. A median septum is not present. The virgella divides a short distance from the sicula aperture into four branches, all of which are broken.

Remarks. The dimensions of the specimen agree well with previous descriptions. Both Hutt (1975) and Bjerreskov (1975) noted thecal apertural spines, prolonged into a fine network in the case of the latter's material, on some of their specimens of this species. Štorch (1985), however, observed no such spines, but did note a virgellar meshwork, often covered with a membrane, on about half of his flattened specimens.

Hutt (1975) suggested that *Orthograptus cyperoides* and *O. insectiformis* might be conspecific. The present material of the two species illustrated herein would indicate that this is probably not the case.

'*Orthograptus*' *insectiformis* (Nicholson, 1869)

Plate 1, figs 7, 8, 13

*.1869	*Diplograpsus insectiformis* Nicholson, p. 237, pl. 11, fig. 13.
.1907	*Diplograptus* (*Orthograptus*) *insectiformis* Nicholson; Elles and Wood, pp. 228–229, pl. 28, fig. 7; text-fig. 150.
1970	*Orthograptus* ? sp.; Hutt, Rickards and Skevington, p. 5, pl. 1, figs 8–10.
.1974	*Orthograptus insectiformis* (Nicholson); Hutt, pp. 34–35, text-fig. 9, figs 1–3, 13.
.1974	*Orthograptus insectiformis* (Nicholson); Rickards and Koren', pp. 200–201, figs 1–4.
.1975	*Orthograptus insectiformis* (Nicholson); Bjerreskov, p. 29, text-fig. 10C.

Holotype. By monotypy; specimen figured by Nicholson 1869, pl. 11, fig. 13; BM (NH) Q3113; from the Llandovery of Dob's Linn, Moffat, Scotland.

Material. Approximately 20, mostly fragmentary, specimens.

Description. The rhabdosome increases in dorso-ventral width (excluding spines) from 0·7–0·8 mm at th1[1] to a maximum of 1·2 mm. 2TRD distally is 1·4 mm. The thecae are simple straight tubes with horizontal apertures each of which is furnished with two pairs of gently curved spines (up to 0·75 mm long) directed antero- and posterio-laterally. The sicula bears an ancora of type 3 of Bates and Kirk (1984).

Remarks. The ancora of this species has been described and its possible function discussed by Bates and Kirk (1984).

'*Orthograptus*' *inopinatus* Bouček, 1943 is very similar in its dimensions to '*O.*' *insectiformis*. It differs in its possession of spines projecting from the nema (see illustrations in Štorch 1985).

Subfamily MONOGRAPTINAE Lapworth, 1873
Genus MONOCLIMACIS Frech, 1897

Type species. Original designation; *Graptolithus vomerinus* Nicholson, 1872, emend. Lapworth; from the Coniston Flags of northern England.

Diagnosis. Thecae geniculate, with straight supragenicular walls approximately parallel to the rhabdosome axis. Proximal apertures may be hooked or bear lateral lappets; distal apertures often simpler, of climacograptid appearance, sometimes with genicular hoods.

Monoclimacis sp.

Plate 3, figs 1–3, 7

Material. Several fragments, the majority of which are distal.

Description. Proximal fragments are gently dorsally curved whilst distal fragments are almost straight. The minimum dorso-ventral width observed is 0·45 mm, the maximum is 0·65 mm. 2TRD values lie between 1·4 mm and 2·0 mm, with the lowest 2TRDs being recorded distally. Distal thecae are of fairly typical monoclimacid appearance, with sharp genicula, and genicular hoods growing out from above simple, slightly everted thecal apertures. Supragenicular walls are, however, gently inclined to the rhabdosome axis. One specimen (UCWG935A, Pl. 3, fig. 2) illustrates the change in thecal morphology from hooked at the first theca preserved, such that the aperture faces proximally, to monoclimacid as seen in the distal thecae. This change takes place rapidly, over four thecae, and involves the retreat of both the dorsal and ventral margins of the hook, so that the former disappears and the latter is modified into the genicular hood.

Remarks. The shape of the rhabdosome and the form of the thecae are very similar to those of *Mcl. crenularis* (Lapworth, 1880), which has only been recorded from the *M. convolutus* Biozone. The latter species reaches a greater width and has more widely spaced thecae, particularly distally, than the present material, from which it may have been derived.

Genus PRISTIOGRAPTUS Jaekel, 1889

Type species. Original designation; *P. frequens* Jaekel, 1889, p. 669, pl. 28, figs 1 and 2; from the Silurian of Germany.

Diagnosis. Thecae simple and straight, or almost straight, throughout length of rhabdosome.

Pristiograptus concinnus (Lapworth, 1876)

Plate 2, fig. 4

v*1876 *Monograptus concinnus* Lapworth, pp. 320–321, pl. 11, fig. 1.
v.1911 *Monograptus concinnus* Lapworth; Elles and Wood, pp. 368–369, pl. 36, fig. 5*a–e* (?*f*); text-fig. 240.
1970 *Pristiograptus concinnus* (Lapworth); Rickards, pp. 60–61, pl. 5, fig. 5.
.1975 *Pristiograptus concinnus* (Lapworth); Hutt, pp. 57–58, pl. 12, figs 1, 2, 7, 8.
1988 *Pristiograptus concinnus* (Lapworth); Štorch, pp. 14–15, pl. 6, figs 2–4; text-fig. 2B.

Lectotype. Designated Přibyl 1948, p. 68; specimen figured Lapworth 1876, pl. 11, fig. 1*a*, from the Llandovery of Dob's Linn, Moffat, Scotland.

Material. Three fragments.

Description. The fragments are very gently ventrally or dorsally curved, up to 1·2 mm wide with 2TRDs of 2·1–2·2 mm. The thecae are simple tubes, inclined at *c*. 25° to the rhabdosome axis, with horizontal to subhorizontal apertural margins, and a slight, often rounded, geniculum at the base of the free ventral wall.

Remarks. The slight geniculum, or convexity of the free ventral wall, of the thecae in this species has been widely illustrated. Hutt (1975) and Rickards, Hutt and Berry (1977) considered this feature to suggest that *Atavograptus atavus* (Jones, 1909) was ancestral to *P. concinnus*.

Genus PRIBYLOGRAPTUS Obut and Sobolevskaya, 1966

Type species. Original designation, Obut and Sobolevskaya 1966, p. 33; *Monograptus incommodus* Törnquist, 1899, p. 11, pl. 2. figs 1–5; from the Llandovery of Sweden.

Diagnosis. (emended herein). Rhabdosome usually long and slender with flexuous curvature, but in one species more robust and straight, and in one with stiff dorsal curvature proximally. Sicula known in only one species, where it is small, reaching to about the aperture of th. 1. Thecae are long, slender, and usually inclined at less than 20° to the axis of the rhabdosome. Thecal apertures usually furnished with lateral lappets (producing 'horns' in pyrite internal moulds), although in one species the distal thecae are of simple pristiograptid form, but with slightly introverted apertures. Thecal apertures usually overhung by a geniculum and, in two species at least, also by a genicular hood.

Remarks. The author recognizes that it is not correct taxonomic procedure to emend a generic diagnosis on a species other than the type species, but feels that emendation is justified in this instance as the internal moulds of the thecae of *Pr. incommodus* and the proximal thecae of *Pr. leptotheca* are so similar.

EXPLANATION OF PLATE 2

Figs 1 and 3. *Agetograptus* sp., 1, UCWG919D, distal end of rhabdosome; note the sheath-like structure surrounding the nema, × 50. 3, UCWG919D, proximal end; note that the aperture of th1[2] opens distally to that of th2[1], × 40.
Fig. 2. *Agetograptus primus* Obut and Sobolevskaya, 1968. UCWG959D, proximal end, × 40.
Fig. 4. *Pristiograptus concinnus* (Lapworth, 1876), UCWG958A, rhabdosome fragment; note slight genicula, × 10.
Figs 5–10. *Pribylograptus leptotheca* (Lapworth, 1876). 5, UCWG909C. proximal fragment, × 15. 6, UCWG925B, mesioproximal fragment, × 15. 7, UCWG913A, mesiodistal fragment, × 15. 8, UCWG910A, distal fragment, × 15. 9, UCWG913A, rounded genicular hood of mesiodistal theca, × 50. 10, UCWG909C, proximal theca, × 100.
All scanning electron micrographs.

LOYDELL, Swedish Llandovery graptolites

Rickards (1976) discussed this genus in detail and included within it *Monograptus incommodus* Tornquist, 1899, *M. argutus* (Lapworth, 1876), *M. leptotheca* Lapworth, 1876, *M.* cf. *incommodus* sensu Hutt and Rickards 1970, and *M. sandersoni* Lapworth, 1876. The present author is in favour of the retention of those forms with proven or inferred lateral apertural lappets with the genus, i.e. *M. incommodus*, *M. argutus argutus* and *M. leptotheca*, and, in addition, probably *M.* cf. *incommodus* sensu Hutt and Rickards 1970 and *M. sandersoni*. Until more detailed studies of the thecal apertures of *M. jonesi* Rickards, 1970, *M. argutus sequens* Rickards, 1970, and *M. angustus* Rickards, 1970 are carried out, their assignation of this genus must be, at most, questionable.

Pribylograptus leptotheca (Lapworth, 1876)

Plate 2, figs 5–10; Plate 3, figs 4 and 5

*.1876	*Monograptus leptotheca* Lapworth, p. 352, pl. 12, fig. 4.
1911	*Monograptus leptotheca* Lapworth; Elles and Wood, p. 371, pl. 37, fig. 2; text-fig. 242.
v.1968	*Monograptus leptotheca* Lapworth; Rickards and Rushton, p. 268, text-figs 2 and 3.
.1970	*Monograptus leptotheca* Lapworth; Rickards, pp. 68–69, pl. 6, figs 3 and 4; text-fig. 14, fig 37; text-fig. 16, fig. 2.
?p1970	*Monograptus* sp. 2; Hutt, Rickards and Skevington, p. 13, pl. 3, figs 58–62 (*non* figs 56 and 57).
.1975	*Monograptus leptotheca* Lapworth; Bjerreskov, p. 51, pl. 7, figs F and G; text-fig. 16C.
.1975	*Pribylograptus leptotheca* (Lapworth); Hutt, p. 73, pl. 16, figs 1–3, 7.
.1988	*Pribylograptus leptotheca* (Lapworth); Štorch, pp. 28–29, pl. 6, fig. 1; text-fig. 2C.

Lectotype. Strachan (1971, p. 57) has noted that the lectotype designated by Přibyl (1948, p. 73), the specimen figured Lapworth 1876, pl. 12, fig. 4*a*, has not been recognized amongst Lapworth's collection and is probably unrecognizable as a figured specimen.

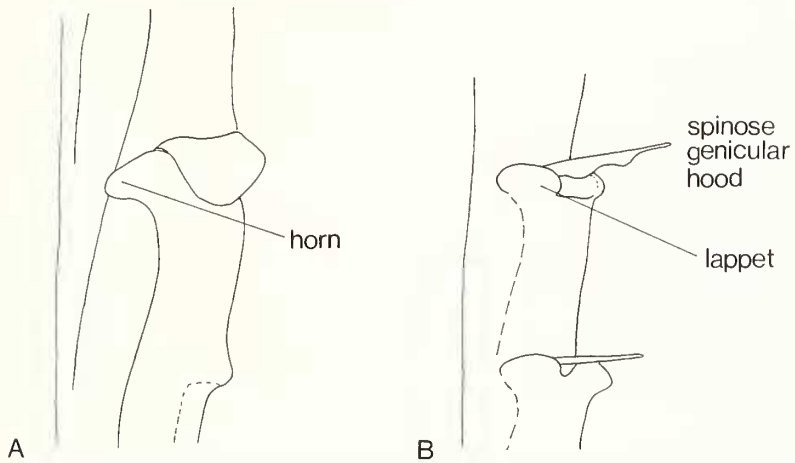
Material. Several hundred proximal, mesial and distal fragments, but possibly belonging to only a few individual rhabdosomes. Most are slightly diagenetically flattened, but some are almost perfectly preserved in three dimensions.

Diagnosis. Rhabdosome more or less straight, of considerable length (probably up to several hundred mm), and with a dorso-ventral width proximally of 0·4 mm increasing gradually to a distal maximum of over 2 mm. Thecae biform; proximally the aperture bears a ventral median saddle together with lateral lappets and is overhung by an angular geniculum furnished with a single-spined genicular hood. Distally the lappets, geniculum and genicular hood retreat until the thecae become simple tubes, although with slight lateral apertural expansion. Overlap of thecae is considerable, increasing from five-eighths proximally to over three-quarters distally. 2TRD is approximately 2·0 mm throughout the rhabdosome. The sicula has not been seen.

Description. The fragments are straight or show slight dorsal curvature. Dorso-ventral width, excluding spines, increases from 0·4 mm proximally to 2 mm distally. Proximal thecae (Pl. 2, figs 5 and 10; Pl. 3, fig. 5) have complex apertures, with a horizontal, median ventral saddle flanked by two distally-directed lateral lappets around which the aperture runs. A broadly triangular genicular hood extending from the angular geniculum of the succeeding theca is furnished with a proximo-ventrally directed spine, 30–40 μm in diameter and with a length of 0·4 mm. Thecal overlap (determined by embedding a rhabdosome fragment in resin and grinding down with carborundum powder) is five-eighths of the thecal length. Distal thecae (Pl. 2, fig. 8; Pl. 3, fig. 4) are simple tubes, inclined at a low angle to the rhabdosome axis, with slightly introverted and slightly laterally expanded thecal apertures. Distal 2TRD is approximately 2·0 mm, with overlap being greater than three-quarters of the thecal length. Both proximal and distal thecae have a ridge running axially along the middle of the ventral wall of the interthecal septum. This may be a preservational feature. The transition from proximal to distal thecal morphologies takes place gradually in the mesial portion of the rhabdosome (Pl. 2, figs 6, 7, 9) and involves the retreat firstly of the genicular spine and then of the genicular hood, accompanied by the retreat also of the lateral lappets, together with a 'smoothing out' of the geniculum. The sicula has not been seen.

Remarks. Rickards and Rushton (1968) and Bjerreskov (1975) have described well-preserved pyrite internal moulds of this species, but misinterpreted the proximal thecal structure. Their apertural transverse 'horns' and 'hood' are, respectively, a pyrite infilling of the lateral lappets, and of the area between the median saddle and the genicular hood. Text-figure 1 compares the appearance of an internal mould with an isolated specimen. That the genicular spine has not been recognised previously, despite some described specimens (e.g. those of Rickards and Rushton 1968) having some preserved periderm, is surprising. However, as Hutt (1974, p. 35) notes, 'spines may easily be overlooked or inadvertently destroyed when examining specimens preserved in full relief.' The fact that, before examination of the Kallholen fauna, spines had not been recorded on the thecae of *Agetograptus prinus*, *Monograptus millepeda* and *M. communis*, the latter two of which are well-known and widely recorded taxa, lends support to Hutt's (1974) observation.

The author agrees with Rickards, Hutt and Berry's (1977) suggested derivation of *Pr. leptotheca* from *Pr. argutus* at the *D. magnus-M. argenteus* Biozone boundary.



TEXT-FIG. 1. *Pribylograptus leptotheca* (Lapworth, 1876). A, internal mould of proximal theca (after Rickards and Rushton 1968, fig. 3). B, isolated proximal theca, UCWG926B. Both ×25.

Genus MONOGRAPTUS Geinitz, 1852

Type species. By subsequent designation (Bassler 1915, p. 822): *Lomatoceras priodon* Bronn, 1835, p. 56, pl. 1, fig. 13; from the Silurian of Germany.

Remarks. Detailed discussion of the use and scope of the genus *Monograptus* is to be found in Rickards (1970), Bulman and Rickards (in Bulman 1970) and Bjerreskov (1975).

Monograptus communis communis Lapworth, 1876

Plate 3, figs 6 and 10

p1876 *Monograptus convolutus* Hisinger, sp. Var. (*a.*) *communis* Lapworth, p. 358, pl. 13, fig. 4*a* (*non b*).

p1913 *Monograptus communis* (Lapworth); Elles and Wood, pp. 480–481, pl. 49, fig. 1*a*, *c* (*non b*, *d*, *e*); text-fig. 336*a* (*non b*).

.1958 *Monograptus communis communis* Lapworth; Sudbury, pp. 520–522, pl. 23, figs 97–101; text-figs 18 and 20.

1970 *Monograptus communis communis* Lapworth; Rickards, pp. 84–85, pl. 6, fig. 7; text-fig. 17, figs 1, 19, ?9.

?p1982 *Monograptus communis* Lapworth, 1876; Lenz, pp. 67–69, figs 5F, G, T and 21G, H, J, L.

Lectotype. Designated by Elles and Wood 1913, explanation to pl. 49, fig. 1*a*; specimen figured by Lapworth 1876, pl. 13, fig. 4*a*, and by Elles and Wood 1913, pl. 49, fig. 1*a*; BU1684*a*; from the Lower Birkhill Shales of Dob's Linn, Moffat, Scotland.

Material. Rare fragments, up to *c*. 5 mm in length.

Description. Proximal fragments are gently dorsally curved, whilst distal ones are almost straight. The thecae are triangular and hooked, with the free ventral wall inclined at *c*. 20° to the rhabdosome axis. The thecal apertures face proximo-dorsally. They are furnished with a pair of proximo-laterally directed spines up to 0·25 mm long. The maximum dorso-ventral width recorded is 1·15 mm. 2TRD is 1·8–2·15 mm.

Remarks. The thecal apertural spines have not previously been observed, although Sudbury (1958) noted a pair of rudimentary lappets on the lateral parts of the dorsal margins of the thecal apertures on her internal moulds of this species. These lappets represent the infilling of the slight outgrowth of the dorsal thecal apertural margin at the base of each spine.

Lenz (1982) describes (but does not illustrate) uncompressed specimens, which he assigned to *M. communis*, from the Cape Phillips Formation, Cornwallis Island, the metathecal portions of which show strong torsion. These must be specimens of a different species, with *M. denticulatus* Törnquist, 1899, a likely candidate. Both Törnquist (1899) and Bjerreskov (1975) have noted that the apertural regions of the distal thecae of the latter species are twisted laterally, always to the reverse side of the rhabdosome.

Rickards, Hutt and Berry (1977) tentatively suggest that *M. denticulatus* was derived from *M. communis*. The morphological information above would suggest that this is unlikely. However, the discovery of spines on the proximal thecal apertures of *M. millepeda*, described for the first time herein, must strengthen their case for this latter species having been derived from *M. communis*, an evolutionary relationship supported by stratigraphical evidence: *M. communis* appears in the *triangulatus* Biozone whilst *M. millepeda* is first seen in the *argenteus* Biozone to which it is confined.

Štorch (1988) has recently identified spines on the thecae of *M. clingani* (Carruthers, 1867) (= *M. communis obtusus* Rickards, 1970) another species which Rickards, Hutt and Berry (*op. cit.*) consider to be derived either from *M. millepeda* or *M. communis*. I would favour derivation from the latter species as overall thecal morphology is more similar. Text-figure 2 illustrates evolution from *M. communis* s.l.

Monograptus denticulatus sensu Sudbury 1958

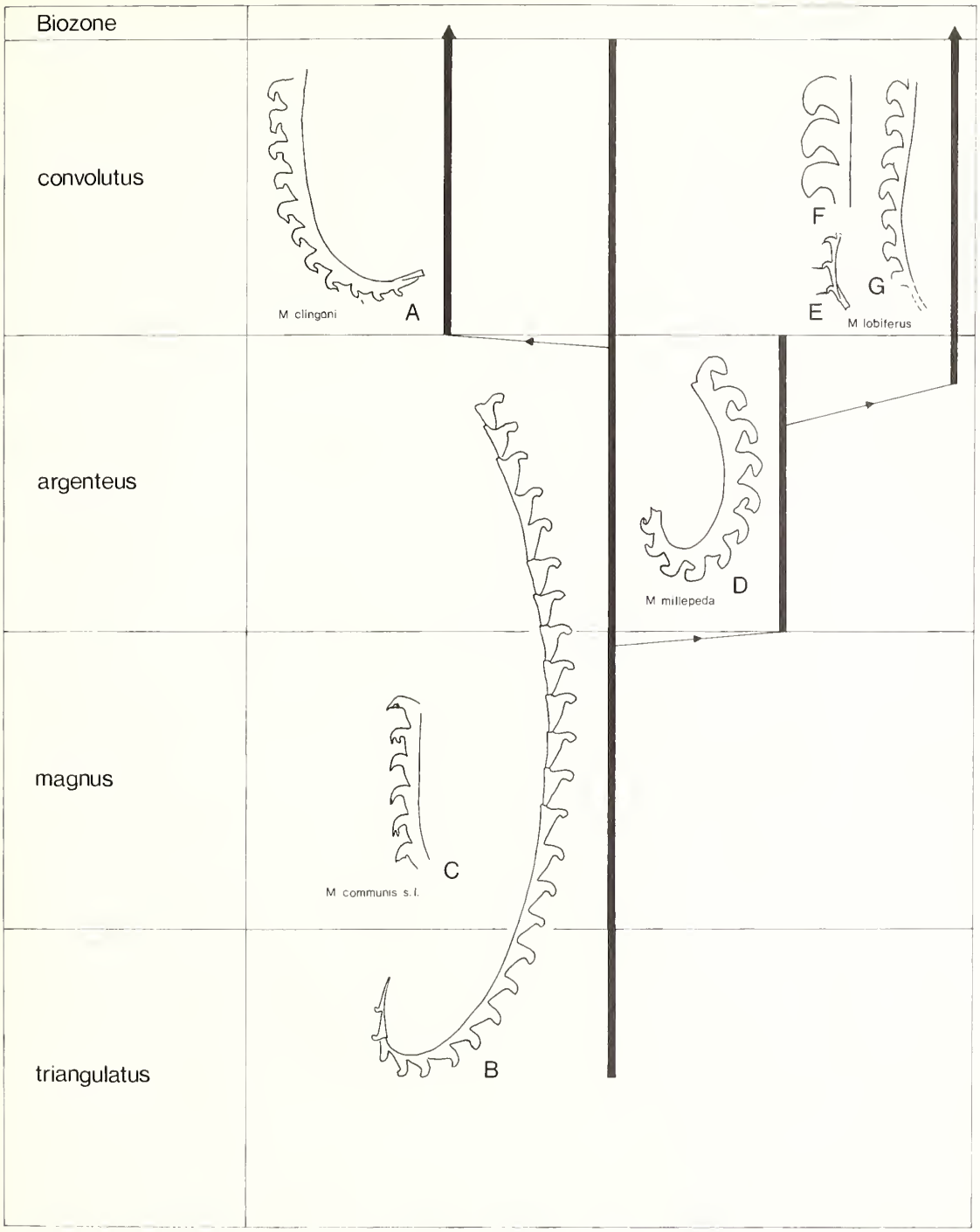
Plate 3, fig. 8

non 1899	*Monograptus denticulatus* Törnquist, p. 18, pl. 3, figs 19–23.
1913	*Monograptus denticulatus* Törnquist; Elles and Wood, pp. 474–475, pl. 48, fig. 2*a*, *b* (?*c–f*); text-fig. 330.
.1958	*Monograptus denticulatus* Törnquist; Sudbury, pp. 509–510, pl. 21, figs 72 and 73; text-figs 4 and 12.
1970	*Monograptus denticulatus* Törnquist; Rickards, pp. 83–84, pl. 7, fig. 3; text-fig. 17, figs 5 and 6.
non 1975	*Monograptus denticulatus* Törnquist; Bjerreskov, pp. 79–80, text-fig. 23B, C.
.1975	*Monograptus denticulatus* Törnquist; Hutt, p. 88, pl. 22, fig. 2; pl. 23, figs 1 and 4.

Material. Approximately 50 fragments, though, due to the tenuity of the prothecae, these bear only one or two thecae.

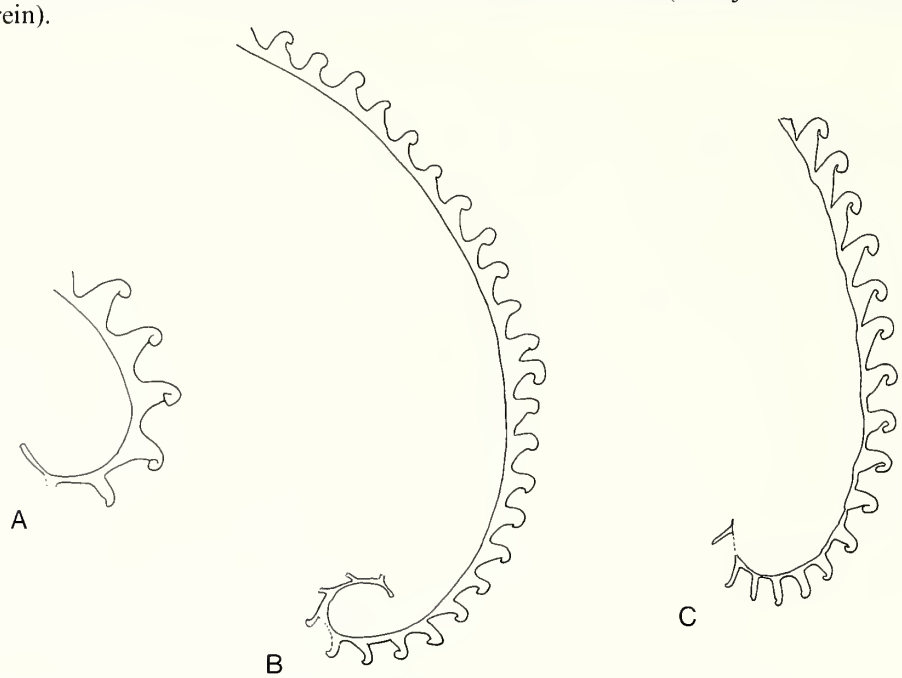
Description. Proximal thecae are rastritiform, whilst distal thecae are more triangular. The protheca is very narrow. Thecal apertures are slightly expanded laterally. They face the dorsal side of the rhabdosome. The maximum dorso-ventral width recorded is 1·25 mm with 1TRD values being 0·95–1·3 mm.

Remarks. The thecal morphology is precisely that interpreted by Sudbury (1958) from slightly compressed material.



TEXT-FIG. 2. Evolution from *Monograptus communis* Lapworth, 1876 s.l. during the Aeronian (= Middle Llandovery). A, *M. clingani* (Carruthers, 1867), after Štorch 1988. B. C, *M. c. communis*; B, after Sudbury 1958; C, UCWG908B. D, *M. millepeda* (M'Coy, 1850), UCWG957A. E–G, *M. lobiferus* (M'Coy, 1850); E, proximal end, after Bjerreskov 1975; F, G, distal and proximal fragments respectively, after Štorch 1988. All × 5.

The thecae of *M. denticulatus* s.s. are less rastritiform proximally, and distally the apertural regions are twisted so as to face the reverse side of the rhabdosome (see Bjerreskov 1975 and Text-fig. 3 herein).



TEXT-FIG. 3. A, B, *Monograptus denticulatus* Törnquist, 1899. A, proximal end, showing twisting of thecal apertures × 10; B, complete rhabdosome, though with damaged proximal metathecae, × 5 (A and B after Bjerreskov 1975). C, *Monograptus denticulatus sensu* Sudbury, 1958, almost complete specimen; note rastritiform proximal thecae, × 5 (after Sudbury 1958).

Clearly, the comments regarding the evolutionary position of *M. denticulatus* given by Sudbury (*op. cit.*) and Rickards, Hutt and Berry (1977) are to the species sensu Sudbury, rather than sensu Törnquist.

Monograptus millepeda (M'Coy, 1850)

Plate 3, figs 9, 11, 14, 15

*.1850	*Graptolites millepeda* M'Coy, p. 270.
.1913	*Monograptus millepeda* (M'Coy); Elles and Wood, pp. 465–466, pl. 46, fig. 10; text-fig. 323.
.1975	*Monograptus millepeda* (McCoy); Hutt, pp. 96–97, pl. 22, figs 1 and 5; text-fig. 19, fig. 4.
v.1978	*Oktavites spinatus*, Ni, pp. 411–412, pl. 3, fig. 20; text-fig. 5, figs 1 and 2.
.1988	*Campograptus millepeda* (McCoy); Štorch, pp. 41–42, pl. 9, fig. 2; pl. 10, fig. 4.

Type specimen. Not traced (see Hutt 1975).

Material. Approximately 150 specimens.

Description. The fish-hook shaped rhabdosome bears laterally expanded, triangular, hooked thecae which do not overlap. The hook is retroverted so that the apertures face proximo-dorsally. The proximal thecae each bear a pair of laterally-directed spines, up to 0·3 mm long. These retreat distally, such that by th10 the thecal apertural margin is smooth and non-spinose. Dorso-ventral width at th1 is 0·45–0·5 mm. The maximum width recorded is 1·2 mm. Distal 2TRD is 1·8–2·2 mm. The sicula is 0·9 mm long. Its apex reaches to just above the top of th1.

Remarks. The proximal thecae of *M. millepeda* have not previously been appreciated as being spinose, although Ni (1978) illustrated thecal spines on the conspecific *Oktavites spinatus.*

It is interesting to note that both Pedersen (1922) and Bjerreskov (1975) illustrate paired thecal apertural spines in *M. lobiferus* (M'Coy, 1850). Bjerreskov (*op. cit.*) noted that they were most obvious in the proximal portion of the rhabdosome. It would thus seem likely that *M. lobiferus* evolved from *M. millepeda* by increased retroversion of the thecal aperture and by reduction in rhabdosome curvature (Text-fig. 2). This is at variance with Rickards, Hutt and Berry's (1977) conclusions. They state that there can be little doubt that the lineage *M.* sp. A (*M.* sp. 1 of Hutt 1975) (*D. magnus* Biozone) to *M. undulatus* Elles and Wood, 1913 (*M. convolutus* Biozone) led to *M. lobiferus.* The derivation suggested herein, from *M. millepeda*, has a sounder biostratigraphical basis, in that *M. lobiferus* first appears in either the *M. argenteus* or the *M. convolutus* Biozone, whilst, to the author's knowledge, *M. undulatus* has only ever been recorded with certainty from the upper part of the *M. convolutus* Biozone. It should be noted here that Štorch (1988) suggested that the *M. lobiferus* group was derived from *Campograptus* Obut, 1949, a genus into which he placed *M. millepeda.*

Genus RASTRITES Barrande, 1850

Type species. By subsequent designation of Hopkinson 1869, p. 158: *R. peregrinus* Barrande, 1850, p. 67, pl. 4, fig. 6; from the Llandovery of Bohemia.

Diagnosis. Rhabdosome with narrow prothecae and straight, completely isolated metathecae, inclined at a high-angle to the rhabdosome axis. The apertures are hooked and laterally expanded in many species.

Rastrites peregrinus Barrande, 1850

Plate 3, figs 12 and 13

*.1850	*Rastrites peregrinus* Barrande, p. 67, pl. 4, fig. 6.
p1914	*Monograptus* (*Rastrites*) *peregrinus* (Barrande); Elles and Wood, pp. 488–489, pl. 50, fig. 1*a–d* (*non e*); text-fig. 343.
.1941	*Rastrites peregrinus peregrinus* Barrande; Přibyl, pp. 4–6, pl. 1, figs 8 and 9; pl. 2, fig. 8; pl 3, fig. 13; text-figs 5 and 6.
1967	*Rastrites peregrinus peregrinus* Barrande; Schauer, p. 176, pl. 2, figs 5–7.
.1975	*Rastrites peregrinus peregrinus* Barrande; Bjerreskov, p. 83, pl. 13, fig. A.

Lectotype. Designated Přibyl 1941, p. 3, as the specimen figured by Barrande 1850, pl. 4, fig. 6; from the Llandovery of Bykoš, Bohemia.

Material. Approximately 50 fragmentary specimens.

Description. Parallel-sided metathecae, with a height of up to 2·35 mm, arise from narrow prothecae. They are inclined at 80–90° to the rhabdosome axis. The thecal apertures are slightly hooked so that the crescentic apertures face proximally. 2TRD lies between 2·0 and 2·5 mm. The proximal end has not been seen.

Remarks. This material agrees well with previous descriptions. The thecal apertural region is considerably less hooked than in many other rastritids and this would support Sudbury's (1958) suggested evolution from *M. triangulatus praedecipiens* Sudbury, 1958, although, as Schauer (1967) and Rickards, Hutt and Berry (1977) suggest, this may have been via *R. socialis* Törnquist, 1907.

PALAEOBIOGEOGRAPHICAL NOTE

Melchin (1989) has recently noted close biogeographical affinities between Arctic Canada and Siberia and, to a lesser extent, China from the middle Rhuddanian (= Lower Llandovery) onwards to the top of the Llandovery. Certain genera and species occurring in the above areas are considered to be absent from Europe. These are the genera *Agetograptus*, *Comograptus* Obut and Sobolevskaya, 1968, and '*Paramonoclimacis*' Wang and Ma, 1977 (*Monograptus sidiachenkoi* (Obut and Sobolevskaya, 1965) and *M. falcata* (Chen and Lin, 1978)) and the species and subspecies *Climacograptus janischewskyi* (Obut, 1949), *Metaclimacograptus orientalis* (Obut and Sobolevskaya, 1966), '*Diplograptus*' *tcherskyi* Obut and Sobolevskaya, 1967 spp., *Lagarograptus inexpeditus* Obut and Sobolevskaya, 1968, *Petalograptus ankyratus* NIGP, 1974, *Monograptus* cf. *M. arciformis* Chen and Lin, 1978, and *M. millepeda curtus* (Obut and Sobolevskaya, 1968). This faunal difference is related by Melchin to the ambient current systems.

It is undoubtedly true that a number of the taxa Melchin (1989) quotes appear to exhibit a distribution which is restricted to Arctic Canada, Siberia and China, including, notably, the highly distinctive *M. sidiachenkoi* and *La. inexpeditus*.

However, the records of *Agetograptus primus* and *Agetograptus* sp. herein (being the first definite records from Europe) necessitate the removal of this genus from Melchin's list of geographically restricted taxa. It should also be noted that Rickards, Hutt and Berry (1977) record *Me. orientalis* from Sweden, and that *M. falcata* may be a junior synonym of *M. argenteus* (Nicholson, 1869), a species widely recorded from Europe.

This is not to say that Melchin's (1989) 'faunal provinces' do not exist, only that the number of geographically restricted taxa involved may be less that he envisages.

Acknowledgements. Special thanks are due to Dr M. G. Bassett who collected the nodules from which the graptolites for this study were isolated and who also provided locality information and to Dr D. E. B. Bates, who initiated the study and assisted with electron microscopy. The research for this work was carried out whilst in tenure of a University of Wales Postgraduate Studentship.

EXPLANATION OF PLATE 3

Figs 1–3, 7. *Monoclimacis* sp. 1, UCWG935A, distalmost thecae of fragment illustrated in fig. 2, ×25. 2, UCWG935A, fragment showing transition from hooked to monoclimacid thecae, ×10. 3, UCWG935A, fourth theca of fragment illustrated in fig. 2, ×50. 7, UCWG935A, first theca of fragment illustrated in fig. 2, ×50.

Figs 4 and 5. *Pribylograptus leptotheca* (Lapworth, 1876). 4, UCWG926A, distal thecae, ventral view, ×15. 5, UCWG909C, proximal theca, ×50.

Figs 6 and 10. *Monograptus communis communis* Lapworth, 1876. 7, UCWG908B, mesial fragment; note thecal spines, ×10. 10, UCWG908B, oblique view of thecal apertures, ×35.

Fig. 8. *Monograptus denticulatus sensu* Sudbury 1958, UCWG923D, fragment of two thecae, ×20.

Figs 9, 11, 14, 15. *Monograptus millepeda* (M'Coy, 1850). 9, UCWG957A, distal thecae of specimen illustrated in fig. 15; note absence of thecal spines, ×20. 11, UCWG941A, showing lateral expansion of metatheca, ×50. 14, UCWG941D, view from proximal end; note thecal spines, ×30. 15, UCWG957A, long fragment, but with damaged proximal end, ×10.

Figs 12 and 13. *Rastrites peregrinus* Barrande, 1850. 12, UCWG924B, rhabdosome fragment with damaged metathecae, ×10. 13, UCWG924A, thecal aperture, ×50.

All scanning electron micrographs.

LOYDELL, Swedish Llandovery graptolites

REFERENCES

BAILY, W. H. 1871. Palaeontological remarks. 22–23. *In* TRAILL, W. A. and EGAN, F. W. *Explanatory memoir to accompany Sheets 49, 50 and part of 61 of the Maps of the Geological Survey of Ireland including the country around Downpatrick, and the shores of Dundrum Bay and Strangford Lough, County of Down*. Alexander Thom, Dublin and London, 71 pp.

BARRANDE, J. 1850. *Graptolites de Bohême*. Théophile Haase Fils, Prague, vi + 74 pp., pls 1–4.

BASSLER, R. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bulletin of the United States National Museum*, **92**, 1–718.

BATES, D. E. B. and KIRK, N. H. 1984. Autecology of Silurian graptoloids. *Special Papers in Palaeontology*, **32**, 121–139.

—— —— ZHAO YU-HONG and LOYDELL, D. K. 1988. Ultrastructural studies on graptolites using scanning electron microscope. *Acta Palaeontologica Sinica*, **27**, 527–543, pls 1–6.

BERRY, W. B. N. 1965. Graptolites, 103–9. *In* KUMMEL, B. and RAUP, D. (eds). *Handbook of paleontological techniques*. Freeman, San Francisco, 852 pp.

BJERRESKOV, M. 1975. Llandoverian and Wenlockian graptolites from Bornholm. *Fossils and Strata*, **8**, 1–94, pls 1–13.

—— 1981. Silurian graptolites from Washington Land, western N. Greenland. *Bulletin Gronlands Geologiske Undersogelse*, **142**, 1–71.

BOUČEK, B. 1943. Über einige gedornte Diplograptiden des böhmischen und sächsischen Silurs. *Mitteilungen der Tschechischen Akademie der Wissenschaften*, **53**, (25), 1–6, pl. 1.

BRONN, H. G. 1835. *Lethaea geognostica*, **1**. E. Schweizerbart, Stuttgart, 768 pp.

BULMAN, O. M. B. 1932. On the graptolites prepared by Holm. 3. The structure of some Monograpti from the Retiolites-Shales of Stygforsen, Dalarne. *Arkiv för Zoologi*, **24A**, (9), 10–15, pl. 6.

—— 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. V1–V163. *In* TEICHERT, C. (ed.). *Treatise on invertebrate paleontology. Part V*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xxxii + 163 pp.

—— and RICKARDS, R. B. 1968. Some new diplograptids from the Llandovery of Britain and Scandinavia. *Palaeontology*, **11**, 1–15.

—— —— 1970. Classification of the graptolite family Monograptidae Lapworth, 1873. V149–V157. *In* BULMAN, O. M. B. 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. V1–V163. *In* TEICHERT, C. (ed.). *Treatise on invertebrate paleontology. Part V*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xxxii + 163 pp.

CARRUTHERS, W. 1867. Graptolites: their structure and systematic position. *Intellectual Observer*, **11**, (4), No. 64, 283–292, pl. 1; (5), No. 65, 365–374, pl. 2.

CHEN, XU 1986*a*. Early Silurian isolated graptolites from Yichang in W. Hubei, China. *Acta Palaeontologica Sinica*, **25**, 229–238, pls 1–3.

—— 1986*b*. On *Streptograptus* and its paleoautecology. *Selected papers from the 13th and 14th Annual Conventions of Palaeontological Society of China*, 115–137, pls 1–3.

—— and LIN, YAO-KUN 1978. Lower Silurian graptolites from Tongzi, northern Guizhou. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **12**, 1–76, pls 1–19.

CHURKIN, M. and CARTER, C. 1970. Early Silurian graptolites from southeastern Alaska and their correlation with graptolite sequences in North America and the Arctic. *United States Geological Survey Professional Paper*, **653**, 1–51, pls 1–4.

CONWAY MORRIS, S. 1981. Parasites and the fossil record. *Parasitology*, **82**, 489–509, pls 1 and 2.

CROWTHER, P. 1981. The fine structure of graptolite periderm. *Special Papers in Palaeontology*, **26**, 1–119.

DUMICAN, L. W and RICKARDS, R. B. 1985. Optimum preparation, preservation, and processing techniques for graptolite electron microscopy. *Palaeontology*, **28**, 757–766.

ELLES, G. L. and WOOD, E. M. R. 1901–18. A monograph of British graptolites. *Monograph of the Palaeontographical Society*, **55** (260), **56** (265), **57** (271), **58** (277), **60** (288), **61** (297), **62** (305), **64** (316), **66** (323), **67** (327), **70** (339), i–clxxi, *a–m*, 1–539, 52 pls.

FORTEY, R. A. 1989. Review of *Early Ordovician (Arenig) graptolites of the Cow Head Group, western Newfoundland, Canada* by S. Henry Williams and Robert K. Stevens. *Palaeontology Newsletter*, No. 2, 44–46.

—— and COOPER, R. A. 1986. A phylogenetic classification of the graptoloids. *Palaeontology*, **29**, 631–654.

FRECH, F. 1897. *Lethaea geognostica*, **1**. *Lethaea Paleozoica*, **1**, **11**, *Graptolithen*. Schweizerbach, Stuttgart, pp. 544–684.

GEINITZ, H. B. 1842. Über die Graptolithen. *Neues Jahrbuch für Mineralogie, Geografie, Geologie und Petrefak.-Kunde*, 697–701, pl. 10.

—— 1852. *Die Versteinerungen der Grauwackenformation in Sachsen und den angrenzenden Länder-Abtheilungen (Die Graptolithen)*, Wilhelm Engelmann, Leipzig, 58 pp., 6 pls.

HALL, J. 1865. *Graptolites of the Quebec Group*. Geological Survey of Canada; Canadian Organic Remains, Dec. 2, 151 pp., text-figs 1–31.

HOPKINSON, J. 1869. On British graptolites. *Journal of the Quekett Microscopical Club*, **1**, 151–166, pl. 8.

HOWE, M. P. A. 1983. Measurement of thecal spacing in graptolites. *Geological Magazine*, **120**, 635–638.

HUTT, J. E. 1974. The Llandovery graptolites of the English Lake District. Part 1. *Monograph of the Palaeontographical Society*, **128** (540), 1–56, pls 1–10.

—— 1975. The Llandovery graptolites of the English Lake District. Part 2. *Monograph of the Palaeontographical Society*, **129** (542), 57–137, pls 11–26.

—— and RICKARDS, R. B. 1970. The evolution of the earliest Llandovery monograptids. *Geological Magazine*, **107**, 67–77.

—— —— and SKEVINGTON, D. 1970. Isolated Silurian graptolites from the Bollerup and Klubbudden stages of Dalarna, Sweden. *Geologica et Palaeontologica*, **4**, 1–23.

JAANUSSON, V. 1973. Morphological discontinuities in the evolution of graptolite colonies. 515–521. *In* BOARDMAN, R. S., CHEETHAM, A. H. and OLIVER, W. A. JR (eds). *Animal colonies: their development and function through time*. Dowden, Hutchinson and Ross, Stroudsberg, USA, 603 pp.

JACKSON, D. E. 1971. Development of *Glyptograptus hudsoni* sp. nov. from Southampton Island, North-West Territories, Canada. *Palaeontology*, **14**, 478–86.

—— and ETHERINGTON, J. R. 1969. New Silurian cyrtograptid graptolites from northwestern Canada and Northern Greenland. *Journal of Paleontology*, **43**, 1114–1121.

JAEKEL, O. 1889. Über das Alter des sogen. Graptolithengesteins mit besonderer Berücksichtigung der in demselben erhalten Graptolithen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **41**, 653–690, pls 28 and 29.

JONES, O. T. 1909. The Hartfell–Valentian succession in the district around Plynlimon and Pont Erwyd (North Cardiganshire). *Quarterly Journal of the Geological Society of London*, **65**, 463–537, pls 24 and 25.

KOREN', T. N. 1968. Novye Rannesiluriiskie graptolity yuzhnogo Uralu. *Paleontologicheskii Zhurnal*, **4**, 101–3. [In Russian].

KURCK, C. 1882. Några nya Graptolitarter från Skåne. *Geologiska Föreningens i Stockholm Förhandlingar*, **6**, 294–304, pl. 14.

LAPWORTH, C. 1873. Notes on the British graptolites and their allies. 1. On an improved classification of the Rhabdophora. *Geological Magazine*, (1), **10**, 500–504, 555–560, Table 1.

—— 1876. On Scottish Monograptidae. *Geological Magazine*, (2), **3**, 308–321, 350–360, 499–507, 544–552, pls 10–13, 20.

—— 1880. On new British graptolites. *Annals and Magazine of Natural History*, (5), **5**, 149–177, pls 4 and 5.

LENZ, A. C. 1974. Evolution in *Monograptus priodon*. *Lethaia*, **7**, 265–272.

—— 1982. Llandoverian graptolites of the Northern Canadian Cordillera: *Petalograptus*, *Cephalograptus*, *Rhaphidograptus*, *Dimorphograptus*, Retiolitidae, and Monograptidae. *Life Sciences Contributions, Royal Ontario Museum*, **130**, 1–154.

—— and MELCHIN, M. J. 1989. *Monograptus spiralis* and its phylogenetic relationship to early cyrtograptids. *Journal of Paleontology*, **63**, 341–348.

MATTHEWS, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16**, 713–719.

M'COY, F. 1850. On some new genera and species of Silurian Radiata in the Collection of the University of Cambridge. *Annals and Magazine of Natural History*, (2), **6**, 270–290.

MELCHIN, M. J. 1989. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences*, **26**, 1726–1746.

—— and LENZ, A. C. 1986. Uncompressed specimens of *Monograptus turriculatus* (Barrande, 1850) from Cornwallis Island, Arctic Canada. *Canadian Journal of Earth Sciences*, **23**, 579–582.

MITCHELL, C. E. 1987. Evolution and phylogenetic classification of the Diplograptacea. *Palaeontology*, **30**, 353–405.

NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, ACADEMIA SINICA (NIGP) 1974. *Handbook of stratigraphy and palaeontology of Southwest China*. Science press, Beijing, 454 pp., 202 pls. [In Chinese].

NI, YU-NAN 1978. Lower Silurian graptolites from Yichang, Western Hubei. *Acta Palaeontologica Sinica*, **17**, 387–416, pls 1–4.

NICHOLSON, H. A. 1868. On the graptolites of the Coniston Flags; with notes on British species of the genus *Graptolites*. *Quarterly Journal of the Geological Society of London*, **24**, 521–545, pls 19 and 20.

—— 1869. On some new species of graptolites. *Annals and Magazine of Natural History*, (4), **4**, 231–242, pl. 11.

—— 1872. *A monograph of the British Graptolitidae. Part 1. General introduction*. Blackwood and Sons, Edinburgh and London, xii + 132 pp.

OBUT, A. M. 1949. *Polevoi Atlas rukovodyashchich graptolitov verchnego silura Kirgizskoy SSR*. Publishing House of the Kirgiz branch of the Academy of Sciences of the USSR, Frunze, 57 pp. [In Russian].

—— and SENNIKOV, N. V. 1980. Graptolitit silura Sibirskoy platformit (llandoveri basseyna rek Gorbiachin i Kylumbe). 3–51, 77–78, pls 1–5. *In* SOKOLOV, B. S., TESAKOV, U. I. and PREDMECHENSKIE, N. N. (eds). *Silur Sibirskoy Platformit, Graptolitit i Chitinozoi*. Izdatelvstvo 'Nauka' Sibirskoe Otdelenie, Novosibirsk, USSR, 88 pp. [In Russian].

—— and SOBOLEVSKAYA, R. F. 1966. Graptolitit rannego silura i Kazachstane. *Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii Geofiziki. Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki*, 1–56, pls 1–8. [In Russian].

—— —— and BONDAREV, R. F. 1965. Graptolitit silura Taymira. *Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii Geofiziki. Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki*, 1–120, pls 1–19. [In Russian].

—— —— and MERKUREVA, A. P. 1968. Graptolitit llandoveri v kernach burovitch skvazhin Norilskogo raiona. *Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii Geofiziki. Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki*, 1–137, pls 1–35. [In Russian].

—— —— and NIKOLAEV, A. A. 1967. Graptolitit i strayigrafiya nizhnego silura okrainnykh podnyatii Kolymskogo Massiva (Severo-Vostok SSSR). *Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii Geofiziki. Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki*, 1–162, pls 1–20. [In Russian].

PACKHAM, G. H. 1962. Some diplograptids from the British Lower Silurian. *Palaeontology*, **5**, 498–526, pls 71 and 72.

PAŠKEVIČIUS, J. 1976. On some new Llandoverian diplograptids of the eastern Baltic. 140–151, pls 1 and 2. *In* KALJO, D. and KOREN', T. N. (eds). *Graptolites and stratigraphy*. Academy of Sciences of Estonian SSR Institute of Geology, Tallinn, 256 pp.

PEDERSEN, T. B. 1922. Rastritesskiferen på Bornholm. *Meddelelser fra Dansk geologisk Forening*, **6**, no. 11, 1–29.

PORTLOCK, J. E. 1843. *Report on the geology of the county of Londonderry, and of parts of Tyrone and Fermanagh*. Andrew Milliken; Hodges and Smith; Longman; Brown, Green, and Longmans; Dublin and London, xxi + 784 pp., 40 pls.

PŘIBYL, A. 1941. O českych a cizích zástupcích rodu *Rastrites* Barrande 1850. *Rozpravy II. Třídy České Akademie*, 51, no. 6, 1–22, pls 1–3.

—— 1948. Bibliographic index of Bohemian Silurian graptolites. *Knihovna Státního Geologického ústavu Republiky Československé*, **22**, 1–97.

RABIEN, A. 1954. Zur Taxionomie und Chronologie der oberdevonischer Ostracoden. *Abh. hess. Landesamt. Bodenforsch.*, **9**, 1–268 [*fide* Matthews 1973].

RICHTER, R. 1948. *Einführung in die Zoologische Nomenklatur*. Kramer, Frankfurt a. M., 252 pp.

RICKARDS, R. B. 1970. The Llandovery (Silurian) graptolites of the Howgill Fells (Northern England). *Monograph of the Palaeontographical Society*, **123** (524), 1–108, pls 1–8.

—— 1976. Classification of *Monograptus*: a redefinition of some Llandovery graptolite genera. 155–163. *In* KALJO, D. and KOREN', T. N. (eds). *Graptolites and stratigraphy*. Academy of Sciences of Estonian SSR Institute of Geology, Tallinn, 256 pp.

—— HUTT, J. E. and BERRY, W. B. N. 1977. Evolution of the Silurian and Devonian Graptoloids. *Bulletin of the British Museum (Natural History)*, Geology, **28**, 1–120, pls 1–6.

—— and KOREN', T. N. 1974. Virgellar meshworks and sicular spinosity in Llandovery graptoloids. *Geological Magazine*, **111**, 193–204, pls 1 and 2.

—— and RUSHTON, A. W. A. 1968. The thecal form of some slender Llandovery *Monograptus*. *Geological Magazine*, **105**, 264–274.

SCHAUER, M. 1967. Biostratigraphie und Taxionomie von *Rastrites* (Pterobranchiata, Graptolithina) aus dem anstehenden Silur Ostthüringens und des Vogtlandes. *Freiberger Forschungshefte*, (*C*), **213**, 171–199.

ŠTORCH, P. 1985. *Orthograptus* s.l. and *Cystograptus* (Graptolithina) from the Bohemian lower Silurian. *Vestník ústředního ústavu Geologického*, **60**, 87–99, pls 1–4.

—— 1988. Earliest Monograptidae (Graptolithina) in the lower Llandovery sequence of the Prague Basin (Bohemia). *Sbornik Geologickych Ved Paleontologie*, **29**, 9–48, pls 1–12.

STRACHAN, I. 1971. A synoptic supplement to 'A monograph of British graptolites by Miss G. L. Elles and Miss E. M. R. Wood'. *Monograph of the Palaeontographical Society*, **125** (529), 1–130.

SUDBURY, M. 1958. Triangulate monograptids from the *Monograptus gregarius* Zone (Lower Llandovery) of the Rheidol Gorge (Cardiganshire). *Philosophical Transactions of the Royal Society of London, Series B*, **241**, 485–554, pls 19–23.

TÖRNQUIST, S. L. 1881. Om några graptolitarter från Dalarne. *Geologiska Föreningens i Stockholm Förhandlingar*, **5**, 434–445, pl. 17.

—— 1890. Undersökningar öfver Siljansområdets graptoliter. I. *Lunds Universitets Årsskrifter*, **26**, 1–33, pls 1 and 2.

—— 1892. Undersökningar öfver Siljansområdets graptoliter. II. *Lunds Universitets Årsskrifter*, **28**, 1–47, pls 1–3.

—— 1893. Observations on the structure of some Diprionidae. *Lunds Universitets Årsskrifter*, **29**, 1–12, 1 pl.

—— 1897. On the Diplograptidae and Heteroprionidae of the Scanian Rastrites-Beds. *Lunds Universitets Årsskrifter*, **33**, 1–24, pls 1 and 2.

—— 1899. Researches into the Monograptidae of the Scanian Rastrites-Beds. *Lunds Universitets Årsskrifter*, **35**, 1–25, pls 1–4.

—— 1907. Observations on the genus *Rastrites* and some allied species of *Monograptus*. *Lunds Universitets Årsskrifter*, (*N.S.*), Afd. 2, **3**, No. 5, 1–22, pls 1–3.

WANG XIAO-FENG, JIN YU-QIN, WU ZHAO-TONG, FU HAN-YIN, LI ZHO-CHONG and MA GUO-GAN 1977. *A palaeontological atlas of central-south China*. Geological Publishing House, Beijing, 470 pp., 116 pls. [In Chinese].

DAVID K. LOYDELL

Institute of Earth Studies
University College of Wales, Aberystwyth
Dyfed, SY23 3DB, UK

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